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THE EVOLUTION OF NEW FORMS IN VIOLA THROUGH HYBRIDISM[1]

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DURING the past eight years I have given much time to the study of our North American violets, not only as represented in large herbaria, but especially as seen in living specimens, both in their natural surroundings and under culture. My garden now contains over 3,500 violet plants of about 650 different numbers or sorts, some 200 of which are from the wild, and 450 raised from seed.

The genus has for over a century been known as difficult and perplexing because of its polymorphism. It has been my good fortune to discover that this is largely due to the frequent occurrence of hybrids between species of the same group. I make out to date some 66 different hybrids that have arisen spontaneously. From about 50 of these I have raised offspring that segregate, often in a surprising manner, reverting variously to the characters of the putative parents of the hybrid. In many cases I have raised from the hybrid two, or even three, generations of offspring.

But not all the anomalous violets that I have grown and propagated can be called hybrids. Hybrids in *Viola* may be known by two marks: first, they are either completely sterile or markedly infertile; secondly, their seedlings are strikingly unlike each other, and often unlike the mother plant. The other class of anomalous violets are normally fertile, and come true to seed; they are often of sporadic occurrence, or if appearing in two or three stations, the stations may be hundreds of miles apart; furthermore, they usually present a mixture of the characters to be found in some two of the species with which they grow. These odd forms, of which I have noted nearly a hundred, are, in my opinion, largely the *result* of hybridism in the remote or recent past. The detailed evidence of this can not be presented in a twenty-minute paper; it demands a printed essay with abundant illustration. I shall here attempt only a brief summary of methods and results.

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[1] This paper was presented before the American Society of Naturalists, in Boston, Mass., December 29, 1909.

I would first call attention to the transitory existence of a hybrid, especially when self-fertilized, as is usually the case in *Viola*. This follows from the laws of Mendel as a mathematical corollary, though I am not aware of any paper in which these deductions have been clearly set forth. Mendel, indeed, showed that in the case of the monohybrid (where the parents differ in only one character) the offspring in the first generation are one half stable, in the second three fourths stable, in the third seven eighths, and so on; until in the tenth generation there is on the average only one hybrid in 1,024 plants. But it can be proved that where the parents differ in *two* characters there will be on the average in the tenth generation only two hybrids in 1,024 plants; where the parents differ in three characters, there will be less than three hybrids in 1,000 plants: where they differ in four characters, less than four hybrids in 1,000; and so on. In the ordinary hybrid over 50 per cent of the offspring in the fourth generation will be stable; in the sixth generation over 85 per cent will be stable; in the eighth generation over 95 per cent; in the tenth generation over 99 per cent. The life of the self-fertilized hybrid is therefore always precarious and relatively brief. The organism is in unstable equilibrium, and is rapidly shifting into conditions of stability.

But the stable forms that emerge are not, as a rule, the forms found in the parents of the original hybrid. They are exclusively such only in the case of the monohybrid; in hybrids of a higher grade the stable forms consist of all possible recombinations of the opposed characters of the parent species. Two species that differ in six characters are capable when crossed of giving rise to 64 distinct and stable forms; if they differ in eight characters, of giving rise to 256 stable forms; if in ten characters, of giving rise to over 1,000.

One or two particular cases must suffice to illustrate how new and stable forms are artificially produced by the propagation of hybrid offspring. In September, 1905, with Mr. Witmer Stone, of Philadelphia, I visited Ivy Hill Cemetery, an interesting violet station, from which the previous May he had sent me several anomalous forms of *Viola.* Two of these proved to be hybrids of a species since named *V. Stoneana;* one with *V. papilionacea,* and the other with *V. triloba. V. Stoneana* has palmately dissected leaves and light-yellow seeds; *V. papilionacea* has undissected leaves, and dark-brown seeds. Among the progeny of their hybrid has appeared a form with the undissected leaves of *V. papilionacea* and the light-yellow seeds of *V. Stoneana.* This form comes true to seed (as was to be expected, since both characters presented are recessive), and shows no longer any marks of hybridity or infertility. Thus has appeared in the garden a stable variety of *V. papilionacea* with light-yellow seeds.

In the second hybrid, *V. Stoneana* × *triloba,* both parents have dissected leaves, though of unlike pattern; but *V. triloba* differs from *V. Stoneana* in being markedly pubescent. The first sowing of the hybrid seed gave me only four plants, one quite glabrous, three quite pubescent. Seeds of these were sown the following year, and from one of the three pubescent plants were obtained nine offspring, all pubescent with the leaf-form of *V. Stoneana.* So here we seem to have a pure dominant—a stable exhybrid—a new and pubescent variety of *V. Stoneana.* Just such a plant was once sent me by Mr. House, collected in the vicinity of Washington.

Leaving now the many cases of dehybridization in *Viola,* that have arisen in a few years of garden culture, let us glance at the evidence that this same process is going on in a state of nature, and has probably been going on for centuries.

Viola cucullata is a well-marked species of wide distribution, but it exhibits many anomalous forms; or as some would say, it is "an aggregate species." The capsules are a clear green in the numerous specimens that I have seen, with one exception. A plant, sent me by Miss Ryon from East Lyme, Conn., has dark-purple capsules; it is quite fertile, breeds true to seed, and in all respects but capsule color is normal *V. cucullata*. How shall we account for this aberrant form? Fortunately, with this plant was sent also from the same colony a hybrid of *V. cucullata* × *sororia*. The latter species at this station, as often elsewhere has very dark-purple capsules; may we not reasonably believe that the purple-fruited *V. cucullata* is a Mendelian product of the hybrid with which it was growing?

Viola cucullata is normally a very glabrous plant. But I have received forms of *V. cucullata* that were decidedly pubescent, from three widely separated stations: Mt. Mitchell, N. C., Milwaukee, Wis., and Salamanca, western N. Y. The plant from Wisconsin has a roundish leaf that resembles that of *V. sororia*, a pubescent species found at the same station. It is quite likely, therefore, that both the leaf-outline and the pubescent peduncles of the aberrant plant have come about through a former cross between the two species.

In October, 1906, I received indirectly from Miss Mulford, of Hempstead, Long Island, a plant of *V. affinis* that had black seeds. The species, which is as widespread as *V. cucullata*, has normally pale-yellow seeds. I noticed that the black seeds of Miss Mulford's plant were also somewhat larger than the ordinary yellow seeds of *V. affinis*. A careful weighing of 200 well-dried seeds of each lot shows the black seeds to be 49 per cent. heavier than the yellow seeds. I surmise, therefore, that the anomalous form is a by-product of *V. affinis* × *papilionacea*, a hybrid from which I have obtained forms in the garden similar to Miss Mulford's. I should add that though the black seed-color is dominant over the pale yellow, two generations of offspring from the Mulford plant show the black color to be stable.

Just the opposite effect has been brought to pass in certain plants of *V. nephrophylla,* a northern species ranging from eastern Quebec to the Rocky Mountains, and having black seeds in all the many specimens seen, except the one here discussed. This plant with buff seeds appeared in a parcel of *V. nephrophylla* sent from Lake Nemahbin, Wis., in 1907, by Dr. Ogden, of Milwaukee. The plant was in all other characters good *V. nephrophylla;* the capsules were crowded with seeds which for two generations have in turn produced plants with like buff seeds. Now from the same region Dr. Ogden sent me a few days later the hybrid *V. affinis* × *nephrophylla,* seeds from which the following year gave plants with buff as well as with black seeds. It is therefore probable that the fertile and stable buff-seeded *V. nephrophylla* from Lake Nemahbin is the descendant of a hybrid of this species with buff-seeded *V. affinis.*

Many similar cases have come under observation. In a limited region in Salisbury, Vt., of less than a square mile, there occurs not infrequently a very pubescent form of *V. latiuscula,* a species which in all other stations I have found to be quite glabrous. On the other hand, from three stations I have obtained perfectly glabrous plants of *V. palmata,* a species normally pubescent. The plants from two of these three stations were somewhat infertile, thus betraying their hybrid origin.

The effect of hybridism is plainly to be seen in the numerous intergradient forms that occur between closely allied species of *Viola.* Take, for example, *V. fimbriatula* and *V. sagittata,* merged into one species by Dr. Gray, probably because of this intergradience. The extreme forms differ chiefly in three particulars: the leaf-blade of *V. sagittata* is narrowly lanceolate, glabrous and coarsely toothed at the base; that of *V. fimbriatula* is oblong-lanceolate, pubescent and not coarsely toothed at the base. But not infrequently we find colonies of *Viola fimbriatula* with leaves that *are* coarsely toothed at the base, and colonies of *V. sagittata* with decidedly pubescent leaves; indeed, this is the prevalent form in the middle west. Where the two species grow together, these and various other interchanges of characters are frequent, in accordance with Mendelian principles of segregation. A like interchange of characters is noticeable in the stemless white violets, *V. blanda*, *V. renifolia* and *V. incognita;* and also in the stemmed yellow violets, *V. pubescens* and *V. scabriuscula.*

We often find in species of wide distribution, as for example *V. affinis* or *V. papilionacea*, numerous forms distinct in one or more characters. Those who are so inclined can break up any one of these species into a dozen or more "elementary species," as some European botanists have done with *V. tricolor.* But there are also certain species of *Viola* that are not polymorphic though of fairly wide distribution; for example, *V. rotundifolia, V. Selkirkii, V. hastata;* and it is worthy of note as bearing upon the thesis of the present paper, that these species have never been found to hybridize.

It frequently happens that a subhybrid form in *Viola* is so unlike either parent of the first-cross as to appear to be specifically distinct. Many such violet hybrids have in recent years been named and published as species: *V. Mulfordæ* Pollard, *V. notabilis* Bicknell and *V. aberrans* Greene are examples. It is surely hazardous in our present knowledge of the genus to put forth as a species a newly discovered form of *Viola*, without studying it through at least one season of growth and through one generation of offspring. It may, indeed, transpire that the new form, though of hybrid origin, is distinct and stable; and if fairly wide-spread, it may be entitled to specific or varietal rank. The bar sinister in the escutcheon of its bastard ancestry may have been quite obliterated. We may be here witnessing the birth of a new species through hybridism. Allow me in closing to present an instance that makes a close approach to these conditions.

In May, 1906, Mr. Stone sent me from Tinicum, Pa., a living violet plant that was quite fertile and appeared a good species. I could not make it out a hybrid, though perhaps predisposed at that time to place an anomalous form in this category. For further light I visited the station with Mr. Stone the following September; but the most careful search failed to reveal another specimen. It soon afterward occurred to me that it might be an offspring of *V. affinis* × *sagittata,* a hybrid which I had found at the same place the year previous, and had transferred to the garden. The two plants, mother and supposed daughter, appeared much unlike, the former being quite infertile, and in most respects an excellent intermediate between the putative parents that grew near by. But careful examination showed that, though no one character of the supposed daughter was intermediate as in the mother, yet *all* were to be found in one or the other of the supposed grandparents. The leaves had the breadth and the rounded basal lobes of *V. affinis,* but the length and the attenuate apex of *V. sagittata;* the capsules were pubescent as in *V. affinis,* but green and large as in *V. sagittata;* furthermore, the peduncles were strictly erect as in *V. sagittata,* not ascending as in *V. affinis;* and also the seeds were brown as in *V. sagittata,* not buff as in *V. affinis.*

The next move was to raise offspring of the plant, to discover if some one of these characters was not impure —in other words, dominant and holding latent the opposed character. The 23 plants subsequently raised showed all the characters of the plant under investigation to be pure excepting two, the pubescence of the capsules and the dark-brown color of the seeds; for glabrous capsules and buff seeds appeared in some of the offspring. The ratio of the four Mendelian forms in the 23 plants was 12: 4: 4: 3, or 9: 3: 3: 2¼, an unexpectedly close approximation to the theoretical ratio 9: 3: 3: 1.

From eleven of these plants another generation of 204 plants was raised the past season. Among these, in addition to the five possible hybrid forms, were obtained also the four possible stable forms. So that I now have fertile plants, free of all hybridity, of four sorts, viz., 18 with pubescent capsules and dark seeds, 9 with pubescent capsules and buff seeds, 18 with glabrous capsules and dark seeds, 44 with glabrous capsules and buff seeds.

Surely, what I have done in the garden, nature might do in the wild, thus evolving a distinct species with three varieties.

In justice to my subject let me say that I am far from maintaining that hybridism is furnishing in the genus *Viola* all the new forms for natural selection to work upon. Hybridism adds no new character to a group of species; it simply recombines in multifarious ways characters already existing. However numerous the patterns that appear in the revolving kaleidoscope, their number is limited; and if we looked long enough we should find them substantially recurring from time to time. To get a strictly new pattern, we should need to insert in the apparatus a new fragment of colored glass. In the evolution of living organisms the new piece of colored glass is what the biologists are considering under the name of mutation.